

THE EYES OF LOWER CAMBRIAN EODISCID TRILOBITES

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ABSTRACT. The oldest known well-preserved trilobite eyes are described in the Lower Cambrian eodiscids *Neocobboldia chinlinica* Lee and *Shizhudiscus longquanensis* S. G. Zhang and Zhu, the latter being slightly older. The material, from south central China, is preserved as moulds or by partial replacement in phosphate, and gives fine details of lens structure. *Shizhudiscus* eyes have biconvex lenses, polygonal and closely packed as in normal holochroal eyes, whereas those of *Neocobboldia* have round, separated lenses, and compare with Middle Cambrian eodiscid eyes previously described as 'abathochroal'. The validity of 'abathochroal eyes' as a separate eye-type is discussed. The lenses of *Neocobboldia*, like those of some phacopids, conform to the ideal model of an aplanatic lens originally described by Des Cartes. Ontogenetic changes in the eyes are described for both species. These show that the programmes for growth of the visual surface and lens emplacement are separate and that the two sometimes got out of phase. The eyes of eodiscids are similar enough to those of other trilobites to suggest that this group is truly trilobitan. They also indicate how advanced the visual organs were at this early stage in trilobite history.

MOST trilobites bear a pair of laterally placed compound eyes, which are of particular interest because the trilobite eye is the most ancient visual system so far known. Although well-preserved trilobite eyes showing details of structure are comparatively rare in the fossil record, it has proved possible to build up a fair understanding of their structure and function. Following the initial studies of Clarke (1889) and Lindström (1901), two types of eye, holochroal and schizochroal have been recognized; a third type, abathochroal, was proposed by Jell (1975) for Cambrian eodiscids. Recent work is summarized by Clarkson (1975, 1979) and Miller and Clarkson (1980).

Schizochroal eyes are believed to have been derived from a holochroal-eyed ancestral type and holochroal eyes are the earliest to appear in the fossil record. But although the record of different kinds of trilobite eyes in the Ordovician and later is good, our knowledge of Cambrian eyes is sparse. In olenelloids, which are considered to be the earliest trilobites found in continuous rock sequences spanning Late Precambrian to early Cambrian times (e.g. in Morocco, North America and Siberia: Fortey and Whittington 1989), the eye may occasionally be preserved. For example, Palmer and Halley (1979, pl. 1, fig. 12) figured the visual surface in *Bristolia* and lenses have been reported in a few meraspides of *Olenellus gilberti* Meek from Alberta (Clarkson 1973, text-fig. 1). Eyes are also present in some Australian Middle Cambrian eodiscids described by Jell (1975), and in Upper Cambrian leptoplastine olenids described by Clarkson (1973). Occasional librigenae with eyes attached belonging to other Upper Cambrian taxa have been figured in various papers, though they have not been studied in detail. The principal reason for the paucity of trilobite eyes in the Cambrian was originally suggested by Öpik (1967): it is that in Cambrian trilobites the visual surface has been bounded by a circumocular suture, comprising the palpebral suture above the eye and the ocular suture below. This circumocular suture, according to Fortey and Whittington (1989), is a primitive character for all trilobites, including agnostoids and olenelloids, and loss of this suture by retention of the eye on the cheek is a derived character. When a trilobite whose eye was bordered by such a suture moulted or died, the visual surface would dehisce entirely and thus would not be preserved. This accords with the observations of Clarkson (1973) who showed that in the olenids the ocular suture became functional only in the adult, and that its retention in many later olenids, and in the vast majority of post-Cambrian trilobites, was due to paedomorphosis. Only because of this fortunate circumstance does the eye in more advanced trilobites remain attached to the librigena, so that it has a good chance of being preserved.

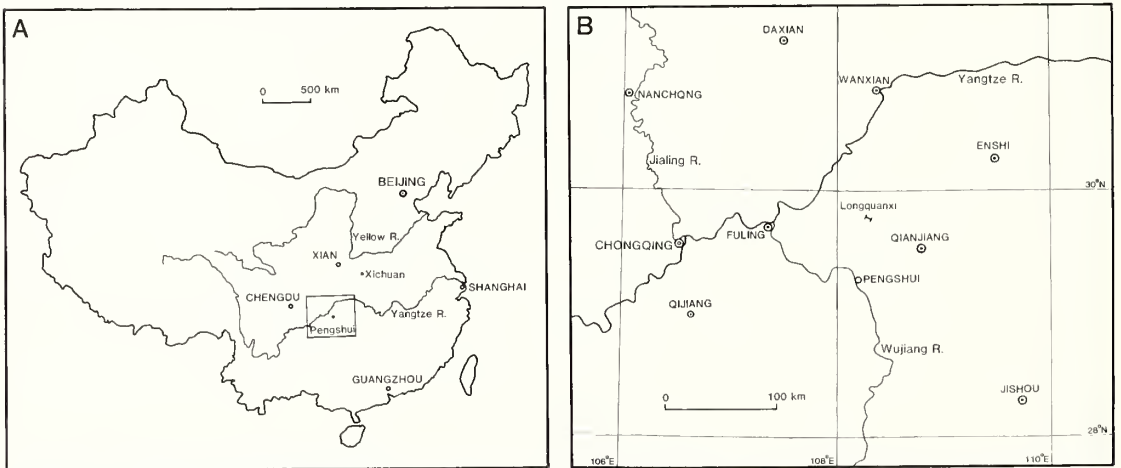
The Cambro-Ordovician Agnostida are generally considered as blind and lacking facial sutures, and ocular structures are known only in *Oculagnostus frici*, as reported by Ahlberg (1988). However, in the Cambrian eodiscid Family Pagetiidae Kobayashi, eyes and proparian sutures have been known for some time, though knowledge of these was limited until Jell's (1975) description of the eyes of *Pagetia* which he proposed as a new type of eye in trilobites – the abathochroal eye. Abathochroal eyes superficially resemble small schizochroal eyes, having a relatively small number of lenses (usually less than 100); these are biconvex and separated from one another. There is, however, no indication of deep intralensar sclera between the lenses, and in this respect they differ from schizochroal eyes proper. Jell (1975) suggests that each lens had its own separate corneal membrane, fixed to the intralensar area round the lens margin. If these differences can be confirmed, then the abathochroal eye can truly be regarded as a distinct type, but our material does not permit a final resolution of this issue.

The two eodiscid genera discussed in this paper both come from the Lower Cambrian of south central China but from different horizons. For both *Neocobboldia* and *Shizhudiscus* large numbers of phosphatized specimens with fine details of structure, and representing several growth stages, have been freed from the enclosing limestone by etching with acid. *Neocobboldia* is restricted to the Canglangpu Stage. Its eyes share a number of distinguishing features with the 'abathochroal' eyes of *Pagetia* described by Jell (1975). *Shizhudiscus* is found at a lower horizon than *Neocobboldia*, in the Qiongzhusi Stage. The eyes of *Shizhudiscus* are the holochroal. They are the oldest known from China, they show clearly many primary characters, and indeed are amongst the most ancient trilobite eyes of all.

LOCALITIES AND STRATIGRAPHY

All specimens described in this paper came from two localities: Xichuan, Henan, and Pengshui, Sichuan (Text-fig. 1A). Since the former locality has been already described and the stratigraphy tabulated in detail (Zhang 1987), only a stratigraphical section (Text-fig. 2) for the latter is given here – the Longquanxi section, which is about 80 km north of Pengshui, in south-east Sichuan (Text-fig. 1B).

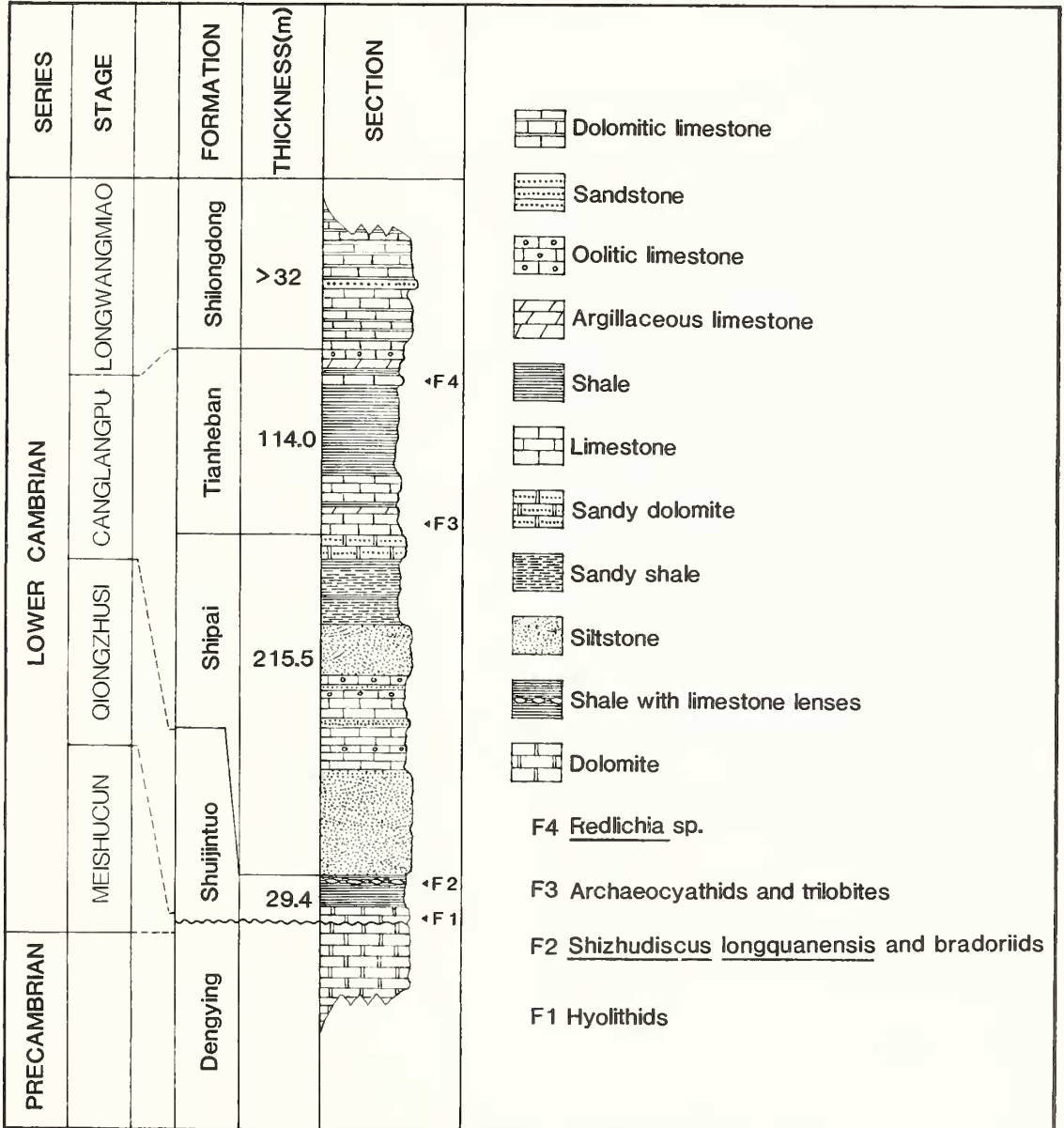
Shizhudiscus is widely distributed in China, and has been recorded from Shaanxi, Guizhou, and Xinjiang as well as from Pengshui, but is always associated with *Eoredlichia*, *Wutingaspis*, and *Zhenbaspis*. All of these have been regarded as of Early Cambrian (Qiongzhusi Stage) age (Lu *et al.* 1982), and this is clearly earlier than *Neocobboldia*. These genera appeared almost at the



TEXT-FIG. 1. Sketch map showing the location ('I') of the Longquanxi section at Pengshui, Sichuan, China, where all specimens of *Shizhudiscus longquanensis* S. G. Zhang and Zhu investigated in this study were collected.

beginning of the trilobite record in China, directly following a horizon of small shelly fossils. Although Brasier (1989) suggests that the base of the trilobite-bearing Cambrian in China is younger than in Morocco and North America, where olenelloids occur, the phosphatized eyes of *Shizhudiscus* that have been obtained are the earliest really well-preserved trilobite eyes so far known from anywhere in the world, and clearly represent a most important stage in their evolution.

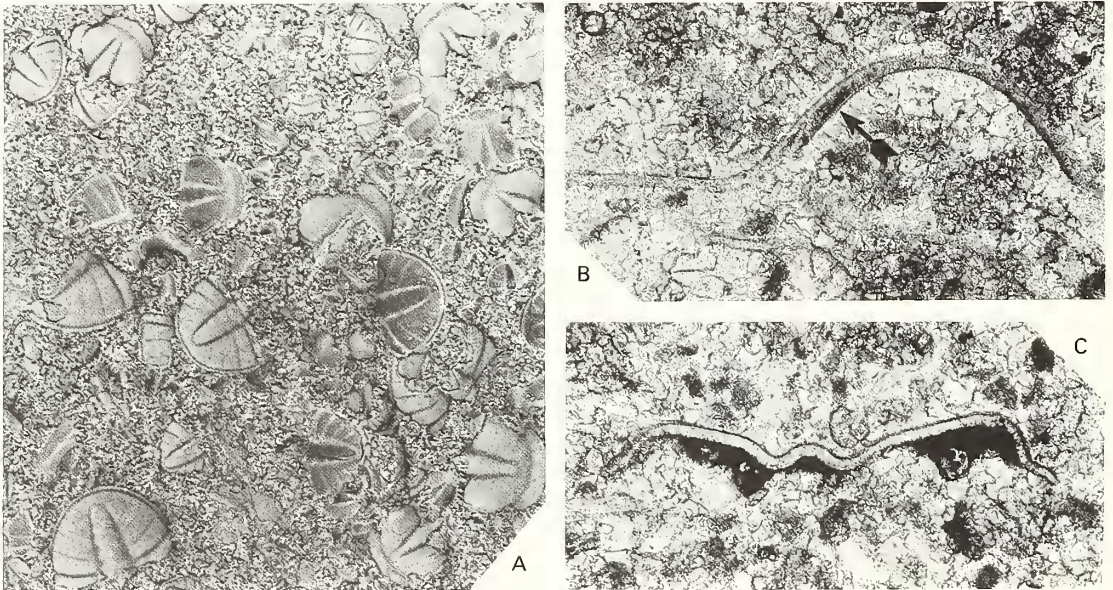
In the Longquanxi section there are about ten thin beds or flat lenses of limestone within black shale. Most of these limestones yield *Shizhudiscus*, but they obviously cover a certain time span. To avoid the possible influence of variation that might arise from a mixed population of individuals that lived at different times, only specimens that came from a single horizon were used in this study.



TEXT-FIG. 2. Columnar section through the Lower Cambrian at Longquanxi, Pengshui, Sichuan, China.

PRESERVATION

The Lower Cambrian trilobites discussed here, *Neocobboldia* and *Shizhudiscus*, have all been preserved by phosphatization and most of them have been extracted from the rock matrix by solution with 3–5% acetic acid. It is very probable that the cuticle was originally composed mainly of calcium carbonate as is the case with other trilobites, but there may have been an additional primary phosphate component. The exuvia are preserved either by encrustation with secondary phosphate, or by replacement of the cuticle itself by phosphate; sometimes there may be both replacement and encrustation. These modes of preservation are evident in specimens dissolved out of the rock, but the extent of phosphatization in our material, even within the same sample is very variable. When a block whose surfaces are replete with trilobite exuvia (Text-fig. 3A) is dissolved in acid, the number of specimens actually recovered as three-dimensional objects may be many fewer than expected. This is because many specimens are hardly phosphatized at all, the others in varying degrees. Thin sections confirm that only some of the specimens have phosphate coats or patches of secondary phosphate within the cuticle. Whether, and to what extent an individual exuvium was preserved by encrustation depended upon a delicate balance of surface chemical conditions.



TEXT-FIG. 3. A, mode of occurrence of *Shizhudiscus* on bedding planes within concretions, Longquanxi section, Gr. I. 69317, $\times 9$. B, thin-section showing both phosphatized black rims on the trilobite cuticle, and invasion of cuticle by phosphate, Gr. I. 69318, $\times 85$. C, thin section showing phosphatized black rims on the cuticle and phosphatic overgrowth on lower surface, Gr. I. 69319, $\times 85$.

Preservation of Shizhudiscus. Where preservation by encrustation has taken place, the secondary phosphate always coats both the internal and external surfaces. What is visible from the outside therefore depends largely upon the relative thickness of the secondary phosphate cover. Where the phosphate is very thin and forms only a light coating on the outer surface, the surface of the eye with its convex lenses is more or less perfectly replicated by the thin phosphate film. Both the internal and the external surface may be preserved in this way. If the secondary phosphate coating is thicker, however, the lenses may be partially or totally obscured.

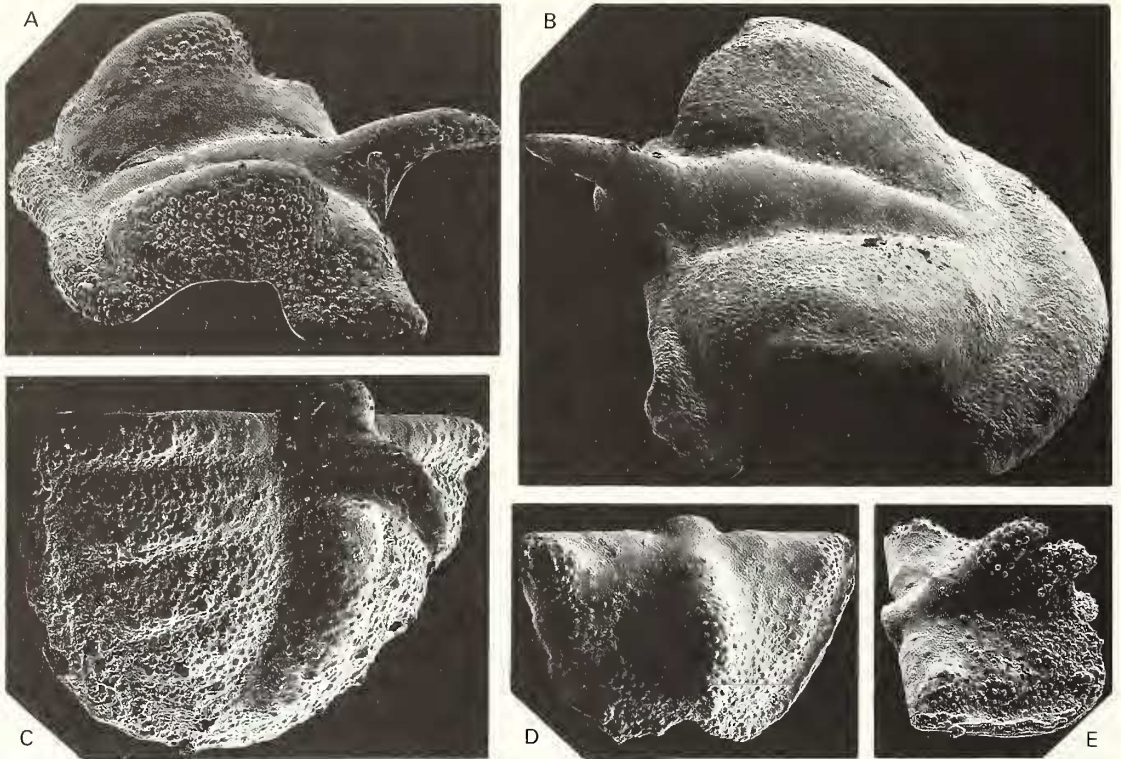
For most specimens of *Shizhudiscus* replacement is common, and specimens usually have both the outer and inner surfaces of the cuticle phosphatized, so that fine details of ornamentation on the outer surface of the carapace is exceptionally well preserved (Text-fig. 4A-E; Pl. 1, figs 8 and 9). This is quite different from that on the surface of the internal layer. In thin section the phosphate replacing both the outer and inner layers shows as a thin opaque film on both the outer and inner surfaces (Text-fig. 2B, C). It seems that the outermost and innermost cuticular layers are easily replaced by phosphate, since it has been found that in many specimens only these layers are altered, leaving the inner parts unchanged (Pl. 1, figs 2, 5, 6, 7). Although most cuticles seen in thin section normally show only black phosphatic rims, there are some instances in which the phosphate shows as a black amorphous mass invading the inner part of the cuticle itself (Text-fig. 3B). In such cases the main internal part of the cuticle could be preserved by replacement. While such phosphatization of the internal cuticle is less common, confirmatory evidence that it does happen comes from acid-etching. The application of a 10% aqueous solution of ethylenediaminetetraacetic acid (disodium salt) to a polished surface of the rock lightly dissolves the carbonate matrix so that the phosphatized outer and inner layers stand up from the surface. While these phosphatic shells replacing the outer and inner surfaces of an individual specimen appear quite distinct, the occasional partial filling or presence of irregular phosphate bars connecting the two layers indicate that the cuticle itself has been phosphatized.

Some specimens, however, have a phosphate coating on their outer surface (Pl. 2, fig. 2), and it is not clear whether the cuticle below it is replaced or not. From a specimen (Pl. 2, fig. 1) directly examined in its rock matrix it is apparent that the outer layer of the eye, which has been partly flaked off, seems too thick to be considered as a single corneal surface. Its thickness may suggest the presence of a phosphate coating. It is of interest to note that this unusual preservation of the eye of *Shizhudiscus* is quite different from that of other known modes of preservation in trilobite eyes, for the inner surface of the lenses has been preserved as a continuous thin layer, running smoothly into the inner surface of the cuticle.

Because the outer layer of the lens is flatter than the inner layer, and the outer surface of the lens may be partially or totally obscured by a phosphate coating (Pl. 2, fig. 2), or to some extent irregular (Pl. 1, fig. 1a), most observations on lens number, morphology, arrangement, and ontogeny have been made with reference to internal moulds of the lentiferous surface.

Preservation of Neocobboldia. Only a few specimens of *Neocobboldia* have been preserved by phosphatic replacement of the cuticle, but these exhibit many details of fine structure on the outer surface (Pl. 3, fig. 1). Most specimens, however, were preserved by encrustation, and the secondary phosphate always coats both the internal and external surfaces. Unfortunately, we have obtained only a very few really small librigenae, and these are almost covered by a thick coating of phosphate. The smaller the specimens, the more thickly they tend to be covered, so that the early stages in ontogeny of the eye are less clear than would be desirable. If the external shell of secondary phosphate is removed, the inner surface of the lens array can be clearly seen as an internal mould (Pl. 3, fig. 8), and likewise the external mould of the surface is visible from the inside. On the whole, the replication of the visual surface as moulds is excellent, and can give near-perfect details of the lens surface, but this depends upon the relative completeness of phosphatization. This is apparent in the series of specimens of *Neocobboldia* illustrated on Plate 3, figures 3-5, which show different degrees of secondary phosphatization. In figure 3 only the proximal parts of the lens surfaces are well preserved, elsewhere the phosphate forms only a dense meshwork; in figure 4 it is more complete, though replication of the whole lens surface is still not quite perfect, whereas in figure 5, the surface of the lenses is an exact mould of the original. In such instances the true shape of the lenses can be appreciated; in the case of *Neocobboldia* they conform to the ideal model of a thick but aplanatic lens, as designed by Des Cartes in 1637 (Clarkson and Levi-Setti 1975).

The presence of so much diagenetic phosphate in these Lower Cambrian rocks is associated with a major global phosphogenic event around the Precambrian/Cambrian boundary (Cook and Shergold 1984). The highest concentrations of phosphate in rocks of this age are actually found in

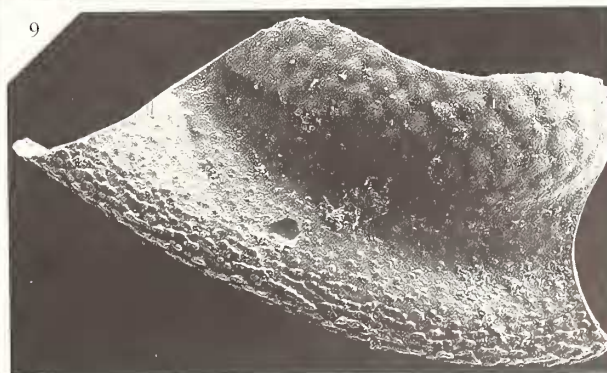
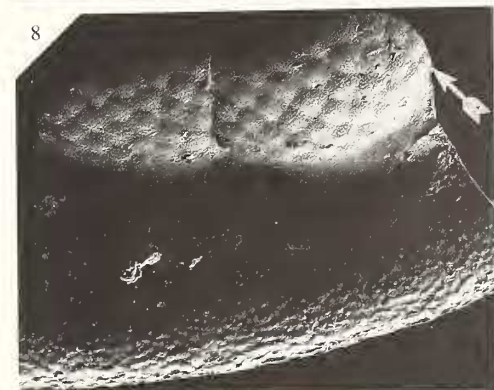
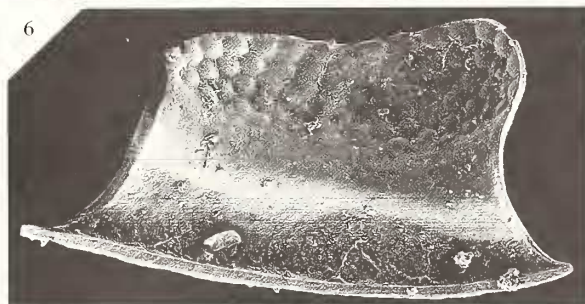
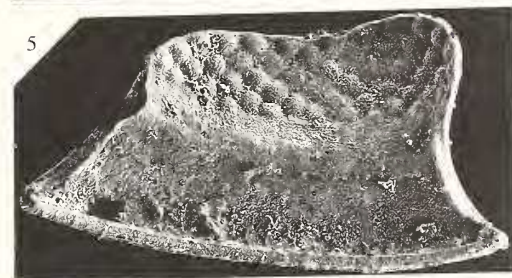
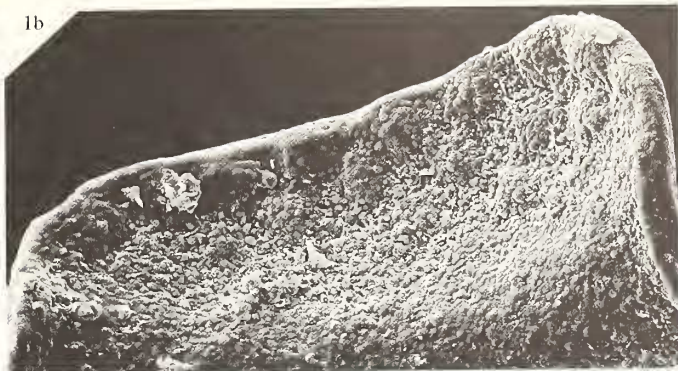
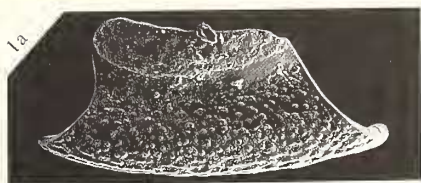


TEXT-FIG. 4. *Shizhudiscus longquanensis*. S. G. Zhang and Zhu, Lower Cambrian, Longquanxi, Pengshui. A, Gr. I. 69251, oblique lateral view of a protaspid cranidium, $\times 128$. B, Gr. I. 69252, oblique lateral view of a holaspid cranidium, showing outline of facial suture, $\times 70.5$. C, Gr. I. 69253, oblique lateral view of a meraspid pygidium, $\times 128$. D, E, Gr. I. 69254, protaspid pygidium; D, dorsal view; E, oblique lateral view, $\times 128$.

southeast Asia, whence our material comes, and Cook and Shergold refer specifically to the Lower Cambrian of southwestern China as one of the major phosphorite areas in the world. The presence of a rich and specialized Early Cambrian eodiscid fauna in southwestern China (Zhang *et al.* 1980) may be associated with very high productivity at this time. The abundance of phosphate was related by these authors to a period of enhanced oceanic overturn, following a long time period when such overturn was slight. This brought nutrients up into the photic zone, and whereas much of the

EXPLANATION OF PLATE I

Figs 1–9. *Shizhudiscus longquanensis* S. G. Zhang and Zhu, Lower Cambrian, Longquanxi, Sichuan. 1a, b, Gr. I. 69255; a, lateral view of smallest right librigena, $\times 123$; b, internal view of same specimen, showing nineteen lenses (including half-lenses) and their pattern of arrangement, partially eroded but still recognizable, $\times 410$. 2, Gr. I. 69256, internal view of a right librigena with twenty-two lenses, $\times 123$. 3, Gr. I. 69257, internal view of a right librigena with thirty-four lenses, $\times 123$. 4, Gr. I. 69258, internal view of a right librigena with forty-two lenses, $\times 123$. 5, Gr. I. 69259, internal view of a right librigena with fifty-one lenses, $\times 123$. 6, Gr. I. 69260, internal view of a right librigena with sixty-nine lenses, $\times 123$. 7, Gr. I. 69261, lateral view of the largest left librigena with ninety-six lenses, $\times 123$. 8, Gr. I. 69262, lateral view of a damaged left librigena showing a half-lens (arrowed) at the posterior margin of the eye. $\times 123$. 9, Gr. I. 69263, lateral view of a left librigena showing the regular arrangement of small lenses, $\times 123$.



phosphate so released was used up in animal and algal metabolism, and for building skeletons, some was made available for diagenesis. The type of preservation we see in the Chinese material is very similar to that noted by Jell (1975*a, b*) in small trilobites preserved during the somewhat later (Middle Cambrian) phosphate 'boom' in Australia.

In general terms, the high-concentration phosphorite episode, which was probably associated with major evolutionary changes at this time, and has allowed such superb preservation, was over long before the Upper Cambrian.

GEOMETRY OF THE VISUAL SURFACE IN TRILOBITES

Our material includes a gradational size series of eyes showing various stages in development for both *Shizhudiscus* and *Neocobboldia*. This has enabled us to work out how the visual surface grows and how the lenses were emplaced. While this is generally similar to that of other trilobite eyes there are some differences in detail, so a brief review of trilobite eye ontogeny and visual surface geometry is given here so that our new information on development of eodiscid eyes can be interpreted in terms of what is already known.

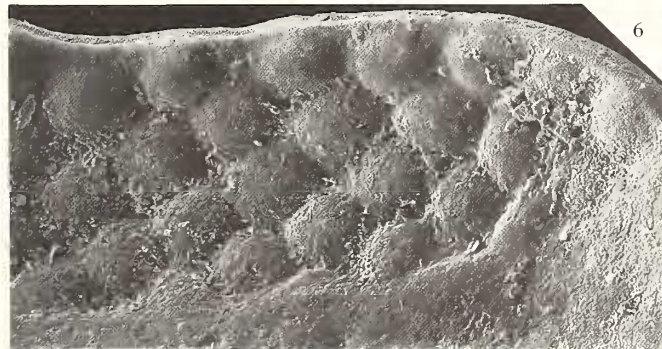
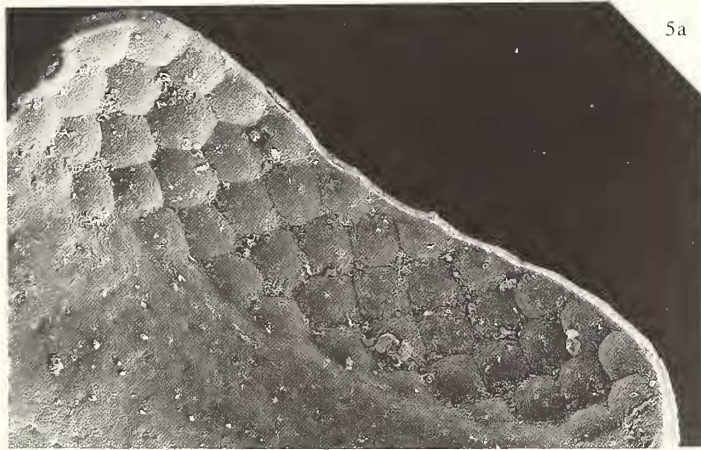
All trilobite eyes known at present, whether holochroal or schizochroal, grow in the same general way (Beckmann 1951; Clarkson 1971, 1975, 1979). They begin their growth as a thin strip of lens-generating cuticle, the generative zone, just below the palpebral lobe. The first horizontal row of lenses is produced from the generative zone which moves downward as the visual surface enlarges, so that new lenses are added at the base of the eye as the generative zone advances, and once produced are permanently 'frozen' into place.

The genetic programme governing the expansion of the visual surface (dominantly downward but also anteriorly and posteriorly) is independent of that governing the emplacement of the lenses, though the two are obviously related. When new space is made at the base of the eye by the generative zone new lenses are formed upon it, but their emplacement follows a defined programme so that they are normally fixed to the bottom of pre-existing files and they will grow until the proximity of neighbouring lenses prevents their further expansion.

In nearly all cases the resultant pattern is a hexagonal close packing system but there are many different versions of this, some involving a change of lens size over the visual surface. Such patterns, many of which have been analyzed in detail (Clarkson 1975) are different answers to the problem of packing lenses in a regular pattern from a single marginal generative zone onto a curving visual surface (Clarkson 1979, p. 6). This is a fundamental problem for the growth of all trilobite eyes including those of the eodiscids, which, while conforming generally to the normal growth patterns, exhibit some striking peculiarities all of their own.

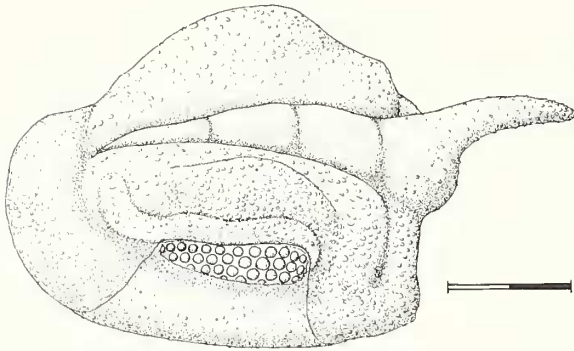
EXPLANATION OF PLATE 2

Figs 1-8. *Shizhudiscus longquanensis* S. G. Zhang and Zhu. Lower Cambrian, Longquanxi, Pengshui. 1, Gr. I. 69264, a librigena within the rock matrix, showing internal moulds of small lenses and partial preservation of their outer surfaces, probably the result of encrustation by secondary phosphate, $\times 128$. 2, Gr. I. 69265, an isolated librigena, showing internal mould of small lenses and secondary phosphate on the outer surface, $\times 176$. 3, Gr. I. 69266, internal view of a right librigena, showing large lenses, $\times 324$. 4, Gr. I. 69267, oblique internal view of a broken eye, showing the inner (black arrowed), and outer (white arrowed) layers of small lenses, $\times 400$. 5*a, b*, Gr. I. 69268; *a*, internal view of a left librigena showing the irregular size and arrangement of the small lenses and the sensory pits below the eye, $\times 272$; *b*, detail of the same eye, showing the two layers of lenses, the separate rounded lenses of the upper row, the polygonal lenses in the centre of the eye, and half-lenses along the lower edge, $\times 680$. 6, Gr. I. 69269, internal view of a left librigena, showing half-lenses along the lower margin of the eye, unequally developed, $\times 400$. 7, Gr. I. 69270, internal view of a right librigena, showing half lenses towards the anterior of the eye, $\times 400$.



MORPHOLOGY AND GROWTH OF THE EYE IN *SHIZHUDISCUS*

Many librigenae of *Shizhudiscus* were available for this study. Unfortunately none of these are preserved in their original position, attached to the cranidium. The cranidium, however, clearly shows the outline of the facial suture, which slopes anteriorly at about 45° , is nearly flat below the palpebral lobe, and descends steeply posteriorly. This constant shape enables isolated librigenae that are bounded by the facial suture to be identified as belonging to the left- or right-hand side of the trilobite (Text-fig. 5). In addition, variation in size of these librigenae indicates that they represent different growth stages. The smallest we have, according to its size and outline, may have separated from a cranidium of late meraspid or early holaspid stage, while some of the larger ones can undoubtedly be referred to the adult stage.

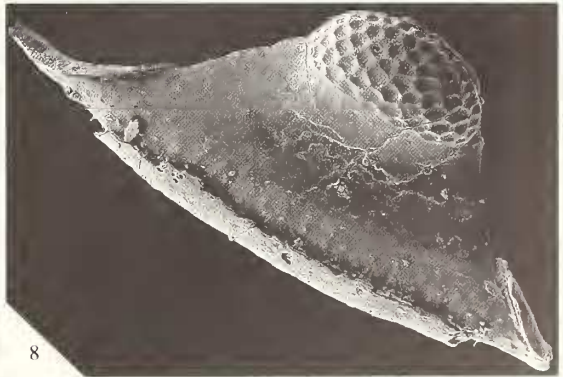
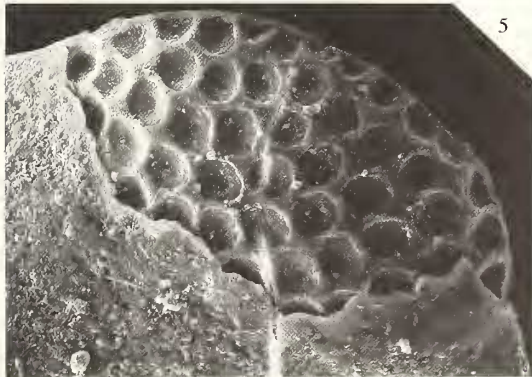
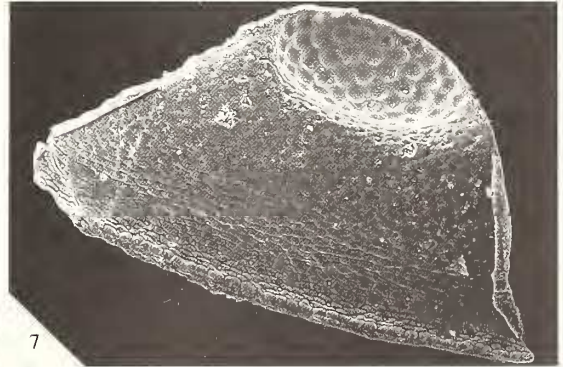
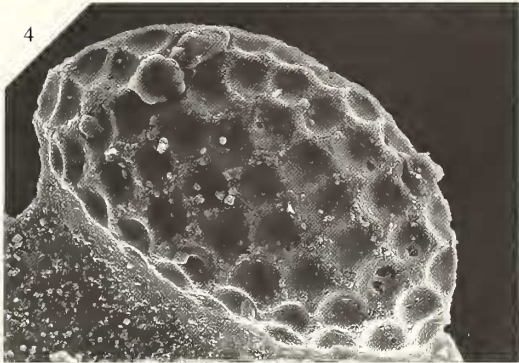
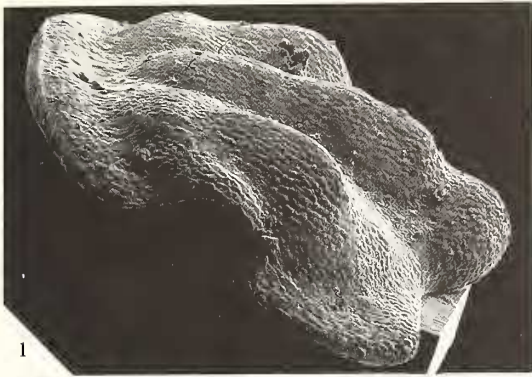


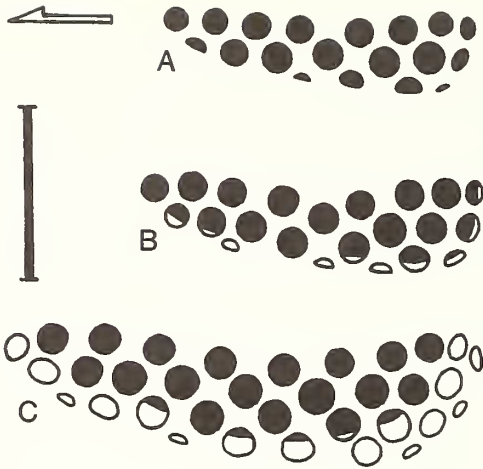
TEXT-FIG. 5. Reconstruction of an early holaspid cephalon of *Shizhudiscus longquanensis* S. G. Zhang and Zhu in oblique-lateral view, showing the left librigena in its original position. Scale bar = 0.2 mm.

The eye of *Shizhudiscus* forms a relatively narrow, elongated band with subparallel upper and lower surfaces, somewhat higher at the rear. It is set at the summit of the librigena, which is about twice the height of the eye itself. The lenses are contiguous and are usually of polygonal form. It has been observed that as the eye grows, it stays much the same shape, always retaining an elongated kidney-shaped outline. Some general principles of growth are evident. Firstly, it is readily seen that as the librigenae increase progressively in size, so the lenses gradually become larger. For some small librigenae, the average lens diameter ranges from 19–25 μm and for some of the largest ones the range is from 30–45 μm . Secondly, the smaller the specimen, the fewer the lenses it bears. A comparison of the different growth stages represented in the series shows how the lenses are emplaced (Text-fig. 6).

EXPLANATION OF PLATE 3

Figs 1–8. *Neocobboldia chinlinica* Lee. Lower Cambrian, Xichuan, Henan. 1, Gr. I. 69300, oblique lateral view of a meraspid cranidium with minutely ornamented outer layer, showing the arched palpebral suture, $\times 104$. 2, Gr. I. 69301, oblique dorsal view of a holaspid cranidium, showing the arched palpebral suture, $\times 105$. 3, Gr. I. 69302, poor phosphatization of eye, $\times 264$. 4, Gr. I. 69303, incomplete phosphatization of eye, $\times 271$. 5, Gr. I. 69304, perfect phosphatization of eye, $\times 268$. 6, Gr. I. 69305, outer surface of somewhat damaged eye, coated with very thin phosphate and showing separated rounded lenses, also well-preserved internal mould below the flaked-off outer surface, $\times 268$. 7, Gr. I. 69306, external mould of a right librigena, showing the smooth outer surface of the rounded lenses, and minutely ornamented librigena, $\times 112$. 8, Gr. I. 69307, a left librigena with the outer layer and phosphatic coating flaked off; the irregular polygonal packing of the lenses on the internal mould is due to erosion of the originally separated lenses, $\times 104$.





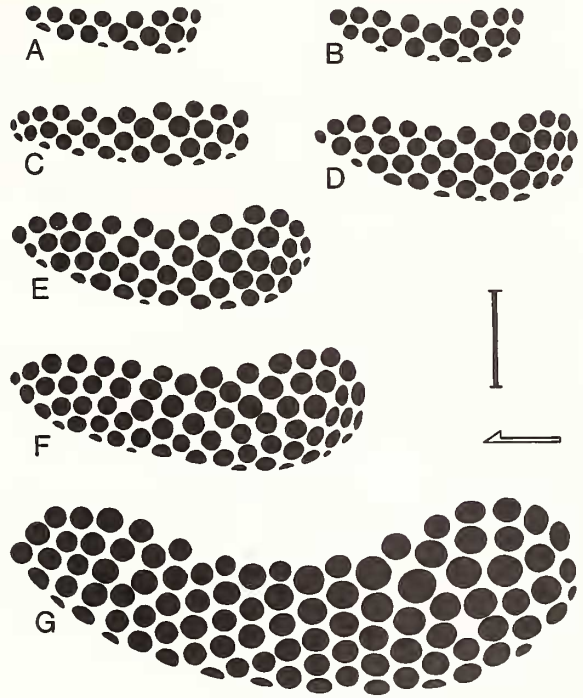
TEXT-FIG. 6. Schematic diagram of early growth stages of the eye of *Shizhudiscus longquanensis* S. G. Zhang and Zhu. A, the smallest librigena with nineteen lenses (including about six half-lenses). B, a somewhat larger librigena with twenty-two lenses: the filled circles or part circles correspond to the lenses or half-lenses in librigena A; the blank parts represent the increase of lenses with growth. C, a still larger librigena with thirty-four lenses, showing lenses or half-lenses corresponding to B (filled circles or part-circles), and the increase in number of lenses with growth; the arrow indicates the anterior. Scale bar = 0.2 mm. See also Text-fig. 7.

The earliest stage in the development of the visual surface must have been the emplacement of a single horizontal row of five or six lenses directly below the palpebral suture. In our smallest specimen, though the phosphate coating is lumpy and irregular so obscuring the details, nineteen lenses (including half-lenses) can be recognized, of which the middle ones are separated laterally from each other by small gaps. These lenses and gaps remain a constant feature throughout the subsequent development of the eye, and can be used as a reference point for tracing the fate of individual lenses. Following the emplacement of the upper horizontal row a second horizontal row is then laid down below it, each of the lenses set between and below the lenses of the upper horizontal row, with the vertical and lateral spacing of the lens centres being about the same. At this stage the upper margin of the eye, along the palpebral suture is virtually flat. As the eye grows, further rows of lenses are added below in regular sequence, but at the same time the eye expands laterally both at the front and the rear. The gradational size series of specimens allows the mode of addition of extra lenses to be established. For while the visual surface is expanding downwards, the upper horizontal row receives new lenses both anteriorly and posteriorly, thus extending itself in both directions, though curving downwards to follow the contour of the facial suture. The upper horizontal row thus retains its apparent identity, though it has grown by accretion in both directions away from the centre.

The lenses that lie along the lower margin of the eye are truncated by the margin of the visual surface so that they appear as semicircular half-lenses. Such half-lenses can sometimes be found also at the posterior (Pl. 1, fig. 8) or anterior (Pl. 2, fig. 8) edges. It has been observed that such half lenses are present in varying degree on every librigena (Pl. 2, figs 3, 5, 7). We consider these to be immature, which implies that, as in other trilobites, the generative zone lies along the anterior, lower, and posterior edges of the eye, and that lenses were emplaced along this generative zone as the eye grew. Two alternative models for growth may be considered. The first is that a single lens could only be fully formed after two moult stages. If this were so, then it may be presumed that the genetic programme responsible for producing new lenses along this margin went into action before each moult. While new, soft cuticle was being formed prior to ecdysis, a number of new lenses and associated visual units below were developing along the lower margin of the eye. The timing of ecdysis was controlled by an over-riding and different programme, which operated when these marginal lenses were imperfectly formed, as represented by the 'half-lens' stage. At the first moult, therefore, they were not fully functional; they only became so after the next moult, by which time they were round and probably were fully functional. The second possibility is that the genetic programme for lens-development was independent of ecdysis so that new lenses continually appeared along the lower margin of the visual surface at any time during growth. This is very

unlikely, however, since the visual surface is shed as a whole unit, and the hardness of the cuticle would inhibit the eruption of new lenses. A zone of half-lenses on the lower margin of the eye is characteristic not only of *Shizhudiscus* but also of *Neocobboldia* and the two specimens of *Pagetia* figured by Jell (1975, fig. 36D). It is not known from other trilobite eyes and seems to be a feature unique to the eodiscids.

TEXT-FIG. 7. Schematic diagram of growth stages of the eyes of *Shizhudiscus longquanensis* S. G. Zhang and Zhu, showing increase in size and number of lenses and expansion of the visual surface with growth. The regular arrangement of the lenses in curving files or rows can be recognized, but irregularities become more pronounced with growth. The arrow indicates the anterior. Scale bar = 0.2 mm.



Over most of the eye the system of lens packing is more-or-less regular, and approximates a pattern of cubic close packing (Text-fig. 7). In such a packing system the lens-centres are equidistant from one another, so that the immediately evident appearance is of two intersecting diagonal rows inclined at 45° to the horizontal but at 90° to each other. The vertical files which form the third intersecting set consist of more widely spaced lenses and are harder to recognize. Cubic close packing is not common in trilobites. Hexagonal close packing on the other hand is normal: it is a more economical system which allows better use of the available space, and the accommodation of relatively more lenses per unit area. The only other recorded example of cubic packing is in the schizochroal-eyed *Phacops turco* aff. *praecedens* Haas, from the Eifelian of Morocco, discussed by Fortey and Morris (1977), which represents a departure from the normal phacopid packing. It is interesting, however, that cubic close packing is found in the eodiscids, which bear the earliest known well-preserved eyes. A cubic system, in which all lens-centres are equidistant is easy to generate. It can be done by a somewhat simpler genetic developmental programme than a hexagonal close packing system. Might this be the reason for cubic packing in the Lower Cambrian? Although the cubic packing system is recognizable, it is never absolutely regular; the vertical files are often sinuous and in places extra lenses seem to be intercalated. Moreover the lenses are larger and less regularly spaced posteriorly, which we interpret as a consequence of developmental constraints imposed by the shape of the visual surface. This must have been controlled by a separate genetic programme to that governing lens-emplacement, and the irregularities seen have developed because the separate genetic 'blueprints' had slightly conflicting instructions.

Anteriorly the facial suture curves downwards fairly gently, whereas at the rear it swings much more sharply downwards in a semicircular curve. It seems that the shape of the facial suture at this point is the primary determinant of the geometry of lens packing towards the rear of the eye, for it imposes a constraint on the number and arrangement of the lenses that can be packed in below it. There is only a limited amount of space in the expanding area enclosed beneath the downwardly curving upper horizontal row, though the curvature of the visual surface in this region, as seen in plan, is higher here than in any other part of the eye, and this allows more room for the lenses that are present to grow. While the regularity of spacing of lens centres breaks down to some extent, these same centres are more widely spaced than in other parts of the eye, and the lenses make use of the available space to grow larger (Pl. 2, figs 3 and 5). The rather unusual lens arrangement is based first on the cubic close packing system, with its 45° inclination of the diagonal rows, rather than the more usual 30° inclination, and secondly on irregularities in the posterior part, mainly determined by geometrical constraints consequent on the form of the facial suture. The later stages in the growth of the eye are illustrated in Text-figure 7. When the maximum depth of the visual surface has been achieved, usually after three or four horizontal rows have been emplaced, the eye still expands laterally, and the final lenses are added at the lower anterior and lower posterior margins. The development of the eye, as in other trilobites, must have operated upon a genetically controlled rolling programme basis. The largest eyes of all still have half-lenses along the base of the eye; presumably these were 'frozen' before their full development had been completed. This happened at each moult stage, and may also have been the case when the trilobite was fully grown, and when the genetic programme which finally ended the development of the eye came into operation.

Although it has not proved possible to measure the angular range of vision in so small an eye as that of *Shizhudiscus* nor to make an accurate stereogram of its visual field (cf. Clarkson 1966a, b, 1975), an eye such as this has a horizontal range of about 70°, the fields of the two eyes not quite meeting at front and rear, and a latitudinal range from just below the equator to about 30° above the sea floor.

MORPHOLOGY AND GROWTH OF THE EYE IN *NEOCOBOLDIA*

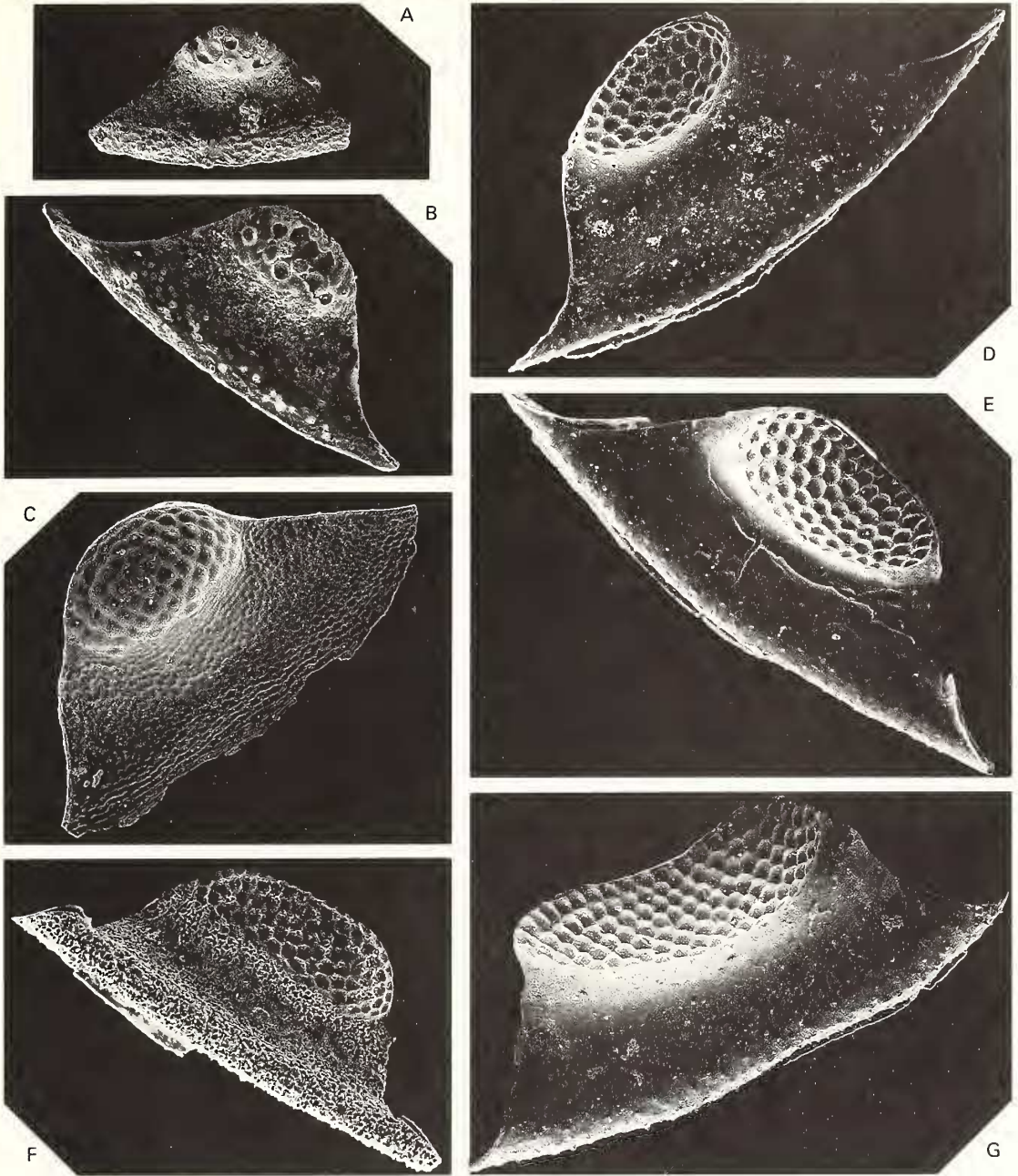
The abundant phosphatized material of *Neocobboldia chinlinica* Lee, from Xichuan, Henan, has enabled all stages in the ontogeny to be worked out in detail and statistically processed (Zhang 1989). The smallest librigena we have (Text-fig. 8A), according to its size and outline, corresponds to a cranidium that has been assigned to an early holaspid stage. The specimens are preserved mainly by phosphatic encrustation and details of structure are normally best established by studying internal and external moulds. In some instances, where the phosphate forms a very thin film or in rare instances of replacement, the external morphology of the visual surface is easily appreciated.

In specimens of average size the eye is an oval body, the dorsal edge of which, bounded by the palpebral suture, is the more strongly curved. Such eyes have about fifty lenses, though some very large specimens, in which the palpebral suture is flatter, may have up to eighty (Text-fig. 8E). The lenses are arranged in a packing system, analyzed below, which is semi-regular. There are three respects in which the eye of *Neocobboldia* differs from that of *Shizhudiscus*:

1. The palpebral suture forms an arch rather than a horizontal line (Pl. 3, figs 1 and 2); a factor which imposes certain constraints upon the geometry of the visual surface.

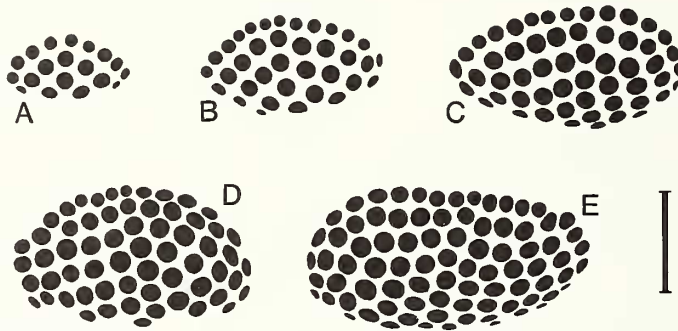
2. The lenses are separated one from another, as is clear both from the outer surface and the internal mould. The eye is thus like that described by Jell (1975) in the eodiscid *Pagetia oculata* as 'abathochroal'.

3. The proximal surface of each lens, in well preserved specimens, has a centrally placed nipple, marked on the internal mould by a corresponding dimple (Pl. 4, figs 3 and 6a, b). Such a lens is similar in form to the ideal thick, but aplanatic lenses designed by Des Cartes in 1637, and detected in the Ordovician phacopid *Dalmanitina* (Clarkson and Levi-Setti, 1975). The latter genus, however, has an additional structure, the intralensar bowl, which in *Neocobboldia* seems to be lacking.



TEXT-FIG. 8. A-E, a series of librigenae of *Neocobboldia chinlinica* Lee, probably representing different holaspide growth stages. Lower Cambrian, Xichuan, Henan; A, Gr. I. 69308, a left librigena with nineteen lenses (including half-lenses); B, Gr. I. 60309, a left librigena with thirty-six lenses, outer surface partially preserved; C, Gr. I. 69310, an external surface of a left librigena with fifty-five lenses; D, Gr. I. 69311, internal mould of a right librigena with sixty-two lenses; E, Gr. I. 69312, an internal mould of a right librigena with eighty-four lenses; the outline of the eye has changed to elongate ovoid. F, G, two librigenae of an unknown genus; F, Gr. I. 69400, a librigena with an elongate eye, composed of eighty-three small lenses in close contact; G, Gr. I. 69401, a larger eye with many small lenses. All $\times 112$.

The visual surface seems to be separable into three zones: an upper row, a central semi-regular zone, and a basal zone of half-lenses. It is possible, by studying individual growth stages, to work out how the lenses were emplaced as the eye grew, but because lens-packing is quite variable from one eye to another (Text-fig. 9), this imposes some limits on interpretation.

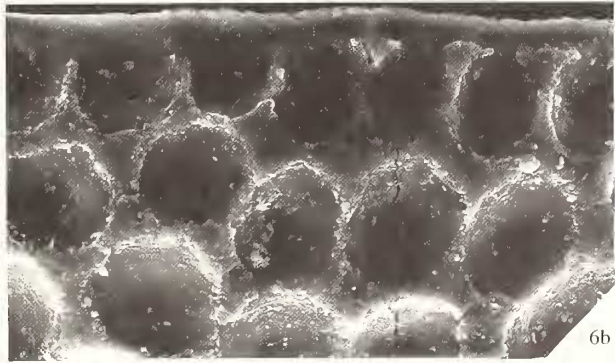
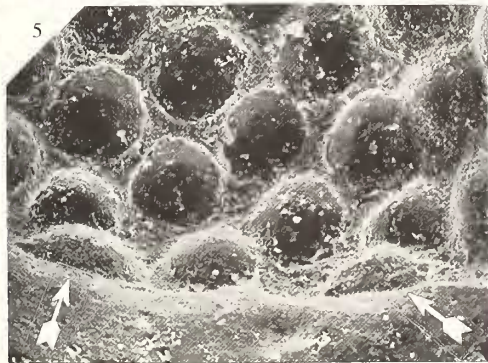
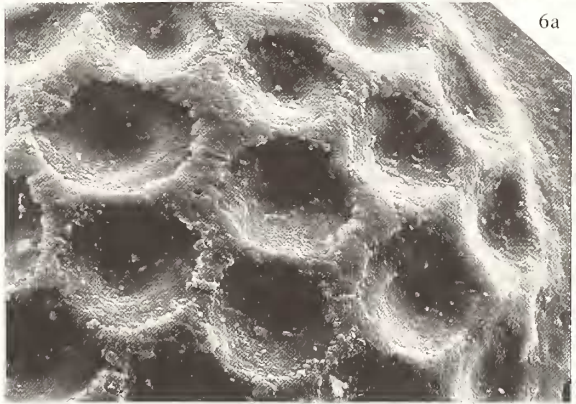
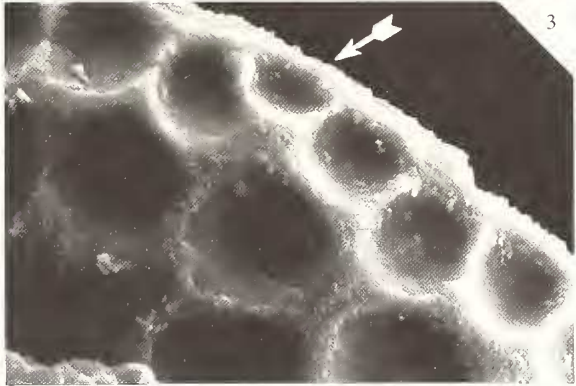
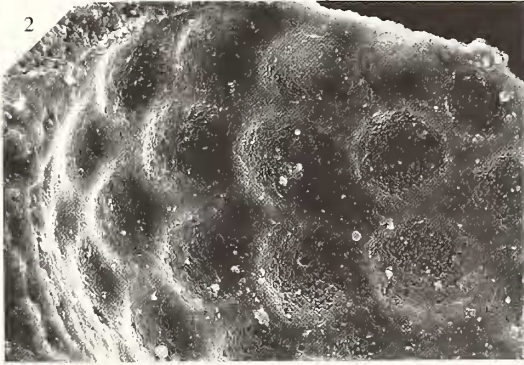
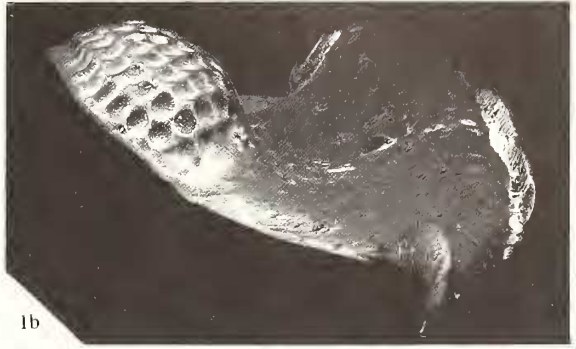
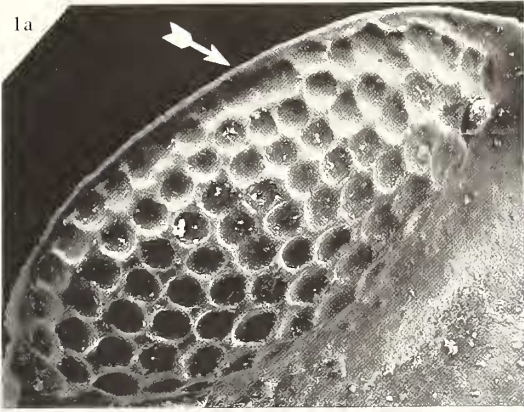


TEXT-FIG. 9. Schematic diagram showing growth stages of the holaspid eye of *Neocobboldia chinlinica* Lee, exhibiting the irregular arrangement of small lenses and change in the outline of the eyes. A, B, E, left eyes. C, D, right eyes. Scale bar = 0.2 mm.

The upper row, lying just below the palpebral suture and equivalent to the upper horizontal row of other trilobite eyes, consists of an arched string of lenses. The central three or four lenses of this chain are usually much smaller than the others of the same row (e.g. Pl. 3, figs 5 and 7; Pl. 4, figs 3 and 6*b*); they are here termed the 'initial set'. Sometimes the upper margin of these lenses is truncated so that they form half-lenses. In many cases this initial set of lenses is separated by a sharp discontinuity in size or level from the neighbouring lenses, anteriorly, posteriorly, or indeed in both directions. In rare instances, the lenses of this initial set are fused together (Pl. 4, fig. 1*a*) as if they had not separated properly during development. The initial set must represent the lenses which formed first, at a larval stage earlier than any represented in our material (our smallest specimens have about twenty lenses). It is clear, both from our gradational size series, and from the morphology of the adult eye, that new lenses were added both to the front and rear of the initial set, so that as the visual surface grew downwards, it also expanded anteriorly and posteriorly, more or less symmetrically, by addition of new lenses below the curving palpebral suture. The upper row in the adult eye has lenses increasing in size in both directions from the centre, and especially where the initial set is well marked, is clearly defined and thus seems rather distinct from the less regular lens-rows below.

EXPLANATION OF PLATE 4

Figs 1-6. *Neocobboldia chinlinica* Lee. Lower Cambrian, Xichuan, Henan. 1*a, b*, Gr. I. 69313, internal mould of a left librigena; *a*, showing the rounded lenses, and the 'fusing' of some of the lenses (including the 'initial set'; arrowed), of the upper horizontal row, $\times 254$; *b*, anterior view, showing the lenses arranged upon a moderately curved spherical surface, $\times 170$. 2, Gr. I. 69306, detail of an external surface, showing rounded, separate lenses, which seem to be covered by a common cornea, $\times 560$. 3, Gr. I. 69314, several small lenses of the 'initial set' (including arrowed lens and adjacent lenses to the right), located in the middle of the upper horizontal row, $\times 880$. 4, Gr. I. 69315, fine annular groove surrounding each lens, on phosphatized internal mould, $\times 560$. 5, Gr. I. 69316, imperfectly developed half-lenses (arrowed) truncated by later half-lenses of the basal zone, $\times 625$. 6*a, b*, Gr. I. 69312, well-preserved internal mould; *a*, showing centrally placed dimple for each lens, $\times 750$; *b*, showing small lenses of the 'initial set' in the middle of the upper horizontal row, $\times 750$.



Under the upper row is a broad, convex zone in which the lenses are arranged in more complex patterns, which vary quite markedly between one eye and another. Perhaps the most immediately evident features are second, third, and other rows, roughly concentric with the upper row, but intercalated lenses usually break down the regularity of arrangement in the lower parts of the eye. The lenses of the second row are usually of more uniform size than those of the upper row, emphasising the apparent difference between the two. Such concentric rows, however, form part of a hexagonal close packing system, which though not fully regular is still fairly well defined, and which seems to have begun to operate automatically, after the formation of the initial set. It is important to note that the visual surface retains its ovoid shape throughout development (at least until the latest stages when it has about eighty lenses and acquires a more elongate form). Thus concentric 'fronts' or zones of growth spread away from the initial set and adjacent lenses, though the variability of the eye of this species makes it difficult to establish the fate of individual lenses by direct comparison.

All the specimens, representing the various growth stages, have a zone of half-lenses along the downwardly bowed lower margin of the visual surface (Pl. 3, figs 3–8; Pl. 4, figs 1*a* and 5), equivalent to those of *Shizhudiscus*, and formed in the same way. There are some examples where lenses towards the base of the eye have themselves been truncated by later lenses. Plate 4, figure 5 clearly shows otherwise rounded lenses with their lower edges overprinted by the last, semicircular, lenses to be formed. Presumably the developmental programme which terminated the growth of the visual surface was not fully synchronized with the programme for lens emplacement; the latter continued for a time after the growth of the visual surface had stopped.

The irregularities which are so evident in all examples studied are of two kinds: those which arise as a normal consequence of packing lenses of fairly uniform size on a visual surface of this shape and those which seem to be abnormal. 'Normal' growth irregularities are widespread in the eyes of trilobites, and arise because of conflicting requirements of different programmes which govern growth (Clarkson 1975, 1979). A more evident malformation, however, is seen in Plate 4, figure 1*a*. This is an example of an eye in which the lenses of the initial set are not properly separated, and this imperfect separation extends some way anteriorly along the upper row. But it is posteriorly from the initial set that the lenses become more haphazardly packed, the irregularity affecting the posterior part of the upper row and also the lenses below it. It is quite probable that this abnormal arrangement may relate to the initial malformation.

In a very few particularly well-preserved specimens a fine annular groove is visible on the phosphatized internal mould of the visual surface surrounding each of the lenses (Pl. 4, fig. 4). These thin rings are preserved on the inner surface of the eye only, and probably represent the site of attachment of sublensar units, presumably of cylindrical form. If this is so, the interior of the eye may well have possessed a series of short, cylindrical capsules, one attached below each lens, as has been envisaged for the schizochroal eyes of *Phacopina*. Perhaps, then the eye is less 'abathochroal' (as envisaged by Jell (1975), whose model suggests that the cornea was anchored at the margin of each lens, on the upper surface) than 'schizochroal' and more similar to the eyes of *Phacopina*.

As with *Shizhudiscus*, the small size of the eyes of *Neocobboldia* precludes accurate measurement of the angular range of vision. Yet, in profile, the eye is much more highly curved (Pl. 4, fig. 1*b*), and subtended a latitudinal range of over 90° from the animal's equator to the pole. The longitudinal range as in *Shizhudiscus* was above 70° for each eye.

THE ROLE OF PAEDOMORPHOSIS AS AN EVOLUTIONARY CONTROL

Heterochrony, that is 'the change through time in the appearance, cessation, or rate of development of ancestral characters' (McNamara 1988), is increasingly recognized as a frequent and important control of trilobite evolution, from Lower Cambrian times onwards. Both paedomorphosis, and more rarely, peramorphosis have been demonstrated. Paedomorphosis (the retention of the juvenile characters of the ancestor as adult characters of the descendant) has recently been reviewed by

McNamara (1986, 1988), who noted three different categories of paedomorphosis and showed how their separate effects enable them to be distinguished.

The eye complex in trilobites was subject to paedomorphic changes and in particular to alteration by neoteny, a reduced rate of development of particular characters relative to that of the rest of the trilobite. Two such examples of neoteny have so far been demonstrated affecting the eye. The first is the retention of the visual surface by the librigena in some leptoplastine olenids as a derived condition (this is a juvenile feature of *Olenus* and allied genera which becomes fairly common in the later leptoplastines: see Clarkson 1973). Secondly, there is the origin of the schizochroal eye from a holochroal ancestral type. It is known that the meraspid eyes of *Paladin* have comparatively few round lenses, large with respect to the visual surface and separated from each other by intralensar sclera. Although this meraspid eye is like a miniature schizochroal eye, this aspect of its morphology is lost in the adult, where the lenses become closely appressed, and the eye becomes holochroal. It is from the juvenile condition that the schizochroal eye is considered to have been derived (Clarkson 1975, 1979).

The process of neoteny, so widespread in the history of the trilobites, may be invoked to account for the differences between the eye of *Shizhudiscus* and the closely related *Neocobboldia*. The eye of *Shizhudiscus* seems to be holochroal and has fairly thin biconvex lenses, all in contact, except for the central ones of the upper horizontal row, and of polygonal form. In contrast, the lenses of *Neocobboldia* are generally rounded and separate. The *Shizhudiscus* eye is here regarded as the 'ancestral' adult holochroal type. That of *Neocobboldia*, however, is interpreted as derived from the juvenile eye of a precursor, whose adult eye was of normal holochroal type, more like that of *Shizhudiscus*. In other words, the process is directly analogous to the envisaged derivation of the schizochroal eyes of phacopid trilobites, though with a lesser degree of specialization. It would be desirable to have confirmation of this from the juvenile eye of *Shizhudiscus*, but the early stages are normally too thickly encrusted by phosphate to allow the relative contiguity of the lenses to be seen. It is clear, however, that the first-formed lenses of the eye of *Shizhudiscus* in the centre of the upper row and the second row are separated one from another; which suggests that in the earliest stages of development the lenses were not in contact.

If it is correct to assume a neotenic origin for the eyes of *Neocobboldia* (and implicitly for the similar 'abathochroal' eyes of *Pagetia* and *Opsidiscus* described by Jell (1975)), it is of particular interest that the lenses conform to an idealized aplanatic Des Cartes model, in which the lower surface of each lens has a central nipple, as do the upper units of the lenses of the early schizochroal eyes of the Ordovician *Dalmanitina*, likewise believed to have risen by neoteny (Clarkson and Levi-Setti 1975). Possibly a similar larval lens structure may have become neotenuously modified in the same way; this is a rather critical area where more evidence may be sought in the future.

COMPARISONS WITH MODERN COMPOUND EYES

Compound eyes in present-day insects and crustaceans consist of radial bundles of cylindrical visual units, the ommatidia. Each of these is capped by a lens, beneath which is a crystalline cone, the main dioptric element. Under the crystalline cone, though not always in contact with it, is the photoreceptive element, or rhabdom. Nerves from the individual rhabdoms link with a large optical ganglion, lying below the ommatidia, in which the overall mosaic image is processed and enhanced.

Exner (1891) proposed that there were two distinct kinds of compound eye, known as apposition and superposition eyes. In apposition eyes the rhabdom is directly connected with the base of the crystalline cone. Each ommatidium is optically isolated from its neighbours and receives light through its individual lens only. These eyes, which are normal in diurnal organisms (and amongst marine crustaceans typical of brachyuran crabs, decapod larvae, and some amphipods and stomatopods) have good resolution, though photon capture is low and the image they form is not very bright. The lenses of apposition eyes are round or polygonal.

Superposition eyes have short spindle-shaped rhabdoms, each set towards the base of its ommatidium, and separated from the lower end of the crystalline cone by a clear zone. In these, light

coming through several adjacent lenses can be focussed on a single rhabdom, and a combined single image is formed at the level of the photoreceptors. Though this image is bright, it is poorly resolved by comparison with that of apposition eyes. Such eyes are characteristic of dark-adapted animals, and visual brightness is achieved at the expense of acuity. In bright light the individual rhabdoms can be isolated from each other by pigment which migrates along the length of the ommatidium to form a sleeve, so that the visual system can also function as an apposition eye.

Superposition eyes could not function unless the dioptric apparatus were able to bend the light rays more strongly than is normal between two media of different refractive index. Since this cannot be achieved by normal refraction, some kind of supplementary dioptric apparatus is needed. It is here that there may be some prospect of useful comparison with trilobite eyes, for the operation of these dioptric elements in crustaceans is directly related to the shapes of the lenses. Three kinds of superposition eyes have now been recognized in crustaceans:

1. *Superposition refracting eyes*. In these eyes, which are typical of mysids and euphausiids, and also of insects, the crystalline cone is a 'lens cylinder' (Exner 1891), in which the refractive index is graded, highest along the axis and lowest along the margins. This system permits light to be bent to a much higher degree than if the crystalline cone had been homogeneous. The cones are circular in cross-section, and the lenses round or hexagonal.

2. *Superposition reflecting eyes*. These eyes are found only in macruran decapods (lobsters, shrimps, etc.). The crystalline cones are 'square-sided plugs of jelly' (Vogt 1975; Land 1976). These act as orthogonal mirrors, and light reflects from their surfaces at twice its incident angle to produce an upright image at the level of the photoreceptor. Land has described them as acting optically as a 'silvered four-sided prism'. These dioptric elements work entirely by mirror-box reflection at their surfaces. They have to be square in cross-section to operate, and eyes of this kind are invariably distinguished by having square lenses.

3. *Superposition parabolic eyes*. Eyes of this kind have recently been described from portunid crabs (Nilsson 1988). They have inwardly-curved parabolic crystalline cones, round or square in cross section. They could easily have originated from apposition eyes.

Recognizing that there are several kinds of modern compound eyes, which can in some respects be distinguished by the shapes of the lenses as seen externally, is there any basis for comparison with eodiscids, or indeed with other holochroal-eyed trilobites? One's first impression might be that if the holochroal eyes of trilobites can be considered as at all similar to those of recent crustaceans, they are likely to have been of apposition type; this is because apposition eyes are the basic type from which various pathways led to superposition eyes of various kinds. The real problem in interpreting them further is that we do not know if the eyes of any trilobites had crystalline cones below the lenses. In crustaceans the cones form the main part of the dioptric system; in trilobites the whole optical function may well have been performed by the lens array alone. If there were cones our interpretation of how the eyes of trilobites worked is likely to be significantly different than if they were not.

Some holochroal eyes had square lenses in the lower part of the eye: *Paralejurus* (Clarkson 1975) and, as shown here, *Shizhudiscus*. Such square lenses originated as a consequence of lens-packing geometry alone. Whereas their shape might suggest that they were pre-adapted for mirror-box optics, the eye needs to be uniformly curved in order for this to work, and this is not the case in trilobites. There is an interesting, though remote parallel here between the development of the larval eye of the decapod *Palaemon serratus* and the eye of *Shizhudiscus*. Land (1981) has shown that in the larval form the eye has hexagonal facets, but as the eye develops these gradually square off. This happens late in development when the animal is two-thirds its adult size, probably relating to a change of habitat and an adult preference for dimmer deeper water. The possibility that the eyes of *Shizhudiscus* and similar forms were other than of apposition type is suggestive, though not as yet compelling. If internal structures of trilobite eyes are one day to be found the whole question can then be re-assessed.

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